TAXONOMY AND BIOLOGY OF FROGS OF THE *LITORIA CITROPA* COMPLEX (ANURA: HYLIDAE)

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ABSTRACT

TYLER, M. J., and ANSTIS, M. 1975. Taxonomy and biology of frogs of the *Litoria citropa* complex (Anura: Hylidae). *Rec. S. Aust. Mus.*, 17 (5): 41-50.

A new species of hylid frog related to *Litoria citropa* is described. The new species inhabits mountainous areas of north-eastern New South Wales and south-eastern Queensland. The tadpoles of both species are described and details of life history are reported. Whereas the adults of *citropa* and the new species are similar, the tadpole mouthparts differ conspicuously.

INTRODUCTION

Litoria citropa is a hylid frog of rather striking appearance and known to occur from north-eastern New South Wales to south-eastern Victoria. The species was known in Victoria from only three specimens (Copland, 1957), until Littlejohn, Loftus-Hills, Martin and Watson (1972) reported on a series collected in East Gippsland. Littlejohn *et al.* provided an analysis of the call, representing the only information on the biology of the species.

Because *L. citropa* is such a distinctive animal and so readily distinguishable from all other Australian species of *Litoria*, we did not envisage that it constituted other than a single species until one of us (M.A.) obtained a series of specimens from Point Lookout in north-eastern New South Wales. These specimens were consistently smaller than those obtained from the central and southern portion of the geographic range, and also differed in the absence of vocal sacs and in having indistinct as opposed to prominent tympana. The subsequent collection of tadpoles introduced an unexpected degree of divergence in what, from adult morphology, we regarded as two closely allied species. Here we define the *L. citropa* complex, describe the new species and report additional biological data.

MATERIAL AND METHODS

The specimens reported here are lodged in the following collections: Australian Museum (A.M.); Department of Zoology, University of Melbourne (M.U.Z.D.); South Australian Museum (S.A.M.).

Methods of measurements of adults follow Tyler (1968). The following abbreviations are employed in the text and in tables: S-V (snout to vent length); TL (tibia length); HL (head length); HW (head width); E-N (eye to naris distance); IN (internarial span); E (eye); T (tympanum).

Descriptions of larval morphology follow the format of Duellman (1970) and use the staging tables of Gosner (1960). Measurements were made to the nearest 0·01 mm with either vernier calipers or an eyepiece micrometer. Abbreviations of larval measurements and their definitions follow: ST (total length, being the distance between the tips of the snout and tail); BL (body length, measured from the tip of the snout to the edge of the intestinal mass).

OBSERVATIONS

Definition of the Litoria citropa complex

Members of the *L. citropa* complex occur only in eastern and south-eastern Australia. They are the only Australian frogs possessing a submandibular dermal gland. This gland is located along the lingual margin of the mandible and is clearly demarcated from the surrounding area in having a protuberant form and smooth surface. The supratympanic fold is also a prominent grandular feature.

The snout to vent length of males ranges from 35 mm to 57 mm, and females from 46 mm to 62 mm. The colour of the dorsum varies from brown to green or gold, and there is always a pronounced dark stripe extending along the

7th March, 1975

canthus rostralis and broadening on the sides of the body. The inguinal region and adjacent portions of the abdomen and lower limbs are usually immaculate yellow or reddish-orange.

Litoria citropa (Tschudi)

Type locality: Port Jackson (Sydney), New South Wales.

Material examined: New South Wales—M.U.Z.D. 47/67, 18 km E. of Braidwood; S.A.M. R13304 A-D, 13339 A-F, 13764: Darke's Forest; M.U.Z.D. 176/63: Flat Rock Ck., Royal National Park; M.U.Z.D. 1593/69: 11 km S. of Kiah; M.U.Z.D. 1518-19/69: 8 km S. of Robertson; M.U.Z.D. 1119-20: 10 km W. of Tomerong; M.U.Z.D. 1792-93/64: Upper Allyn; M.U.Z.D. 582/63: Waterfall, Sydney; M.U.Z.D. 1690-91/64: Wombat Ck., Barrington Tops. Victoria—M.U.Z.D. 1594-97/69: Maramingo; M.U.Z.D. 1590-92/69: Tonghi Ck., 8 km W. of Cann River.

Description: Because detailed descriptions of external morphology have been provided by Copland (1957) and Moore (1961), we have only summarised the variation observed in the specimens examined by us, and devoted the greatest attention to those features unreported or inadequately described previously.

The adult males range in size from 44·4 to 56·6 mm S-V, and gravid females from 56·9 to 61·8 mm S-V. The head is bulbous, rounded and broader than long (HL/HW range 0·87-0·96; mean 0·92). The eye to naris distance is consistently greater than the internarial span (E-N/IN range 1·05-1·44; mean 1·3). The superior border of the tympanum passes beneath the glandular supratympanic fold, but the visible portion is very distinct and has a pronounced annulus.

The fingers are long and slender, with moderately large terminal discs, and either a trace of webbing between the third and fourth fingers or no webbing at all (Fig. 1a). Webbing between the toes is incomplete, reaching the subarticular tubercle at the base of the penultimate phalanx of the fifth toe (Fig. 1b). The hind limbs are of short to moderate length (TL/S-V range 0·50-0·57; mean 0·53).

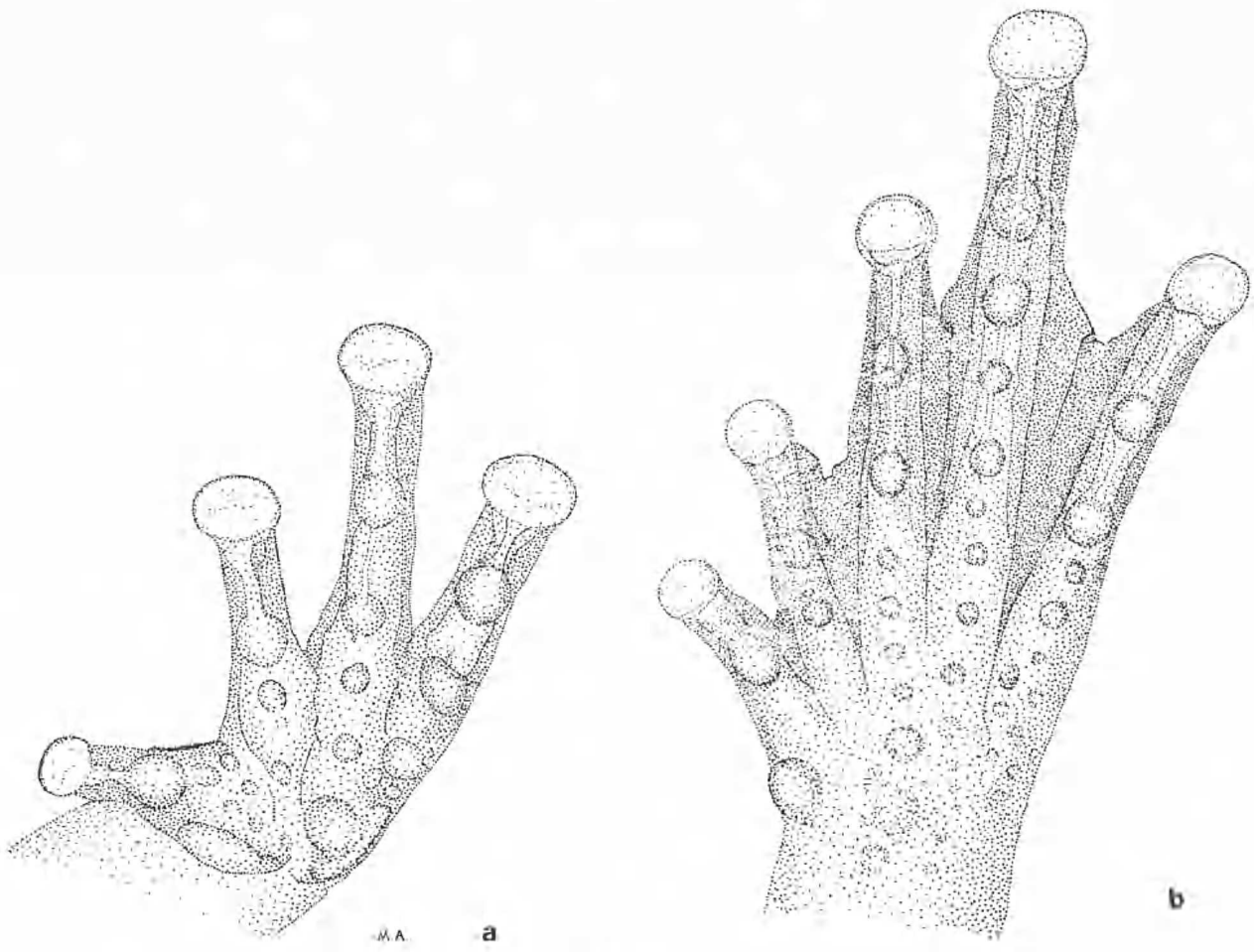

FIG. 1
(a) hand, and (b) foot of *Litoria citropa*.

The vocal sac is a unilobular, submandibular structure confined to the area above the musculus interhyoideus. The size and position of the vocal sac apertures are unique amongst Australian hylid frogs, being very small slits located adjacent to the articulations of the jaws.

The colour in life was described by Kinghorn (1932), and reproduced by Moore (1961). A photograph of a living adult is shown in Figure 2a. Variation of dorsal colours of a live adult includes slate grey with green suffusions, to brown and green or almost pure green. The anterior and posterior surfaces of the hind limbs, the axillary and the inguinal regions are usually deep reddish orange, and the ventral surfaces of the hind limbs are light red.

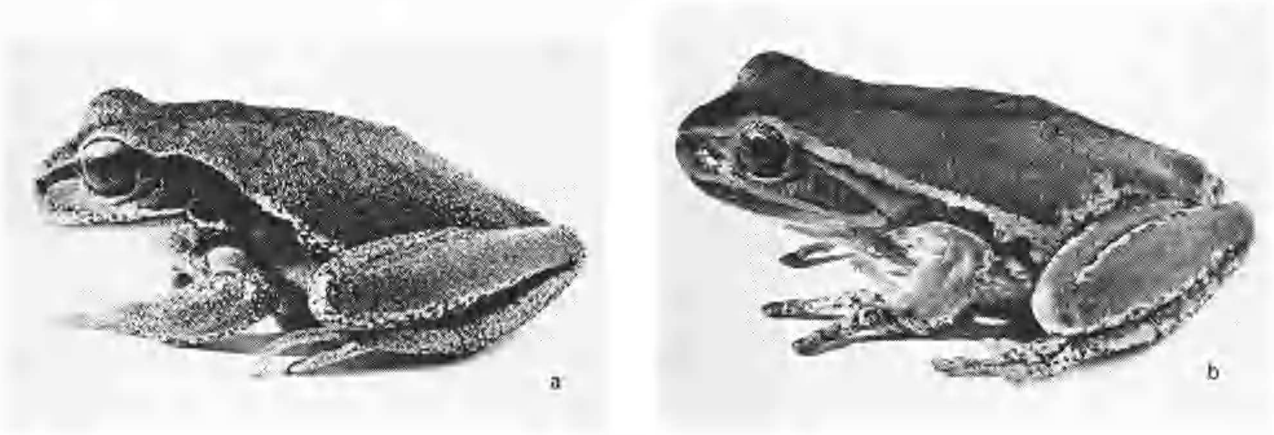

FIG. 2

(a) *Litoria citropa*; (b) *L. glandulosa*.

Some of the specimens examined by us have violet pigmented bones comparable to the condition reported by Tyler (1970) which characterises five other species of frogs occurring in eastern and south-eastern Australia. The pigmentation is most intense in specimens from the extreme south-east of the geographic range: Maramingo, Kiah and Tonghi Creek. Bone pigmentation is very faint or absent in specimens from Tomerong and has not been found in individuals from localities north of Robertson. Absence of violet pigment is in no way associated with the period of time spent in preservative, but is clearly correlated with geography.

Habitat: Specimens were collected over a wide geographic range. The principal field studies, however, took place at Darke's Forest, where adult and/or tadpoles were collected in the following situations: (1) Maddern Creek—a series of broad, deep pools separated by shallow sections of varying flow rates crossing a sandstone base, and sometimes falling into large canyons; (2) The Waratah Creek; and (3) an unnamed creek flowing into the Lodden River.

Plants found along these creeks included species of *Eucalyptus*, *Banksia*, *Acacia*, *Leptospermum*, *Callistemon*, *Hakea*, *Pultenea*, *Persoonia*, *Petrophile*, *Typha*, *Cyperus* and *Ghania*.

Adult Behaviour: Adult males most frequently were collected adjacent to the creeks in Darke's Forest during April, 1971, and September to November, 1972. Dry bulb temperatures recorded on four occasions when frogs were heard calling ranged from 14°C to 19·5°C. During the day frogs were found on sandstone plateaus or outcrops, either beneath or amongst the rocks, and usually fairly close to water. The mating call has been described and analysed by Littlejohn *et al.* (1972). The impression gained was that calling increased on warmer nights following rain when the skies were still overcast.

Breeding is known to occur in September and November and possibly extends until January. Amplexus is axillary.

Life history: Amplexus was observed in a captive pair on the night of 6th-7th November, 1972. The individuals were placed in a plastic container with some water and amplexus was observed at about 20-30 hours. The female uttered a soft release call for some minutes following the onset of amplexus and then remained silent. The specimens were then transferred to a dish containing water, a large, flat sandstone rock and some reeds, and 890 eggs were laid during the night, either singly or in small groups and attached to the surface of the rock or to the floor of the vessel.

The sites of ova deposition in the field were the smooth rocky floors of small pools connected to or separated from the creeks. In all cases the water depth ranged from approximately 10 to 70 mm. The outer capsules of the eggs became covered with fine brown silt within two or three days of deposition.

The eggs have dark brown animal hemispheres, appearing black macroscopically and have creamy white vegetal hemispheres. There are three vitelline membranes.

Measurements of the early stage embryos, capsules and larvae derived from the above mating are listed in Table 1. Initial development was rapid, nerulation was reached early on 9th November, and the tail bud (Stage 17) later on the same day. At this stage a U-shaped groove united two well-formed ventral suckers, above which occurred the stomodeal depression. The body was dark brown and the yolk sac yellowish-brown.

TABLE 1

MEASUREMENTS OF EMBRYOS AND LARVAE OF L. CITROPA AT VARIOUS STAGES

(Means in parenthesis)

EMBRYOS

Stage	Sample	Embryo Diameter (mm)	Capsule Diameter (mm)
2	4	1·68-1·76 (1·73)	5·92-6·48 (6·10)
4-5	5	1·60-1·76 (1·70)	5·44-7·20 (6·18)
5	3	1·70-1·80 (1·75)	5·84-6·48 (6·19)
5-6	3	1·68-1·76 (1·72)	6·08-7·20 (6·45)
8-9	15	1·76-1·84 (1·78)	5·36-6·48 (6·08)
17	15	2·56-3·48 (3·12)	
			Total Length (mm)
19	1		5·68
20	10		5·84-6·56 (6·26)
21-22	9		6·24-7·12 (6·76)
23	3		8·24-8·64 (8·45)
24	3		8·48-9·28 (8·96)
25 (early)	8		8·96-10·16 (9·65)
25 (late)	9		12·48-13·44 (12·92)

LARVAE

Stage	Sample	Body Length (mm)	Total Length (mm)
26	8	5·9-7·8 (6·9)	14·7-20·0 (17·1)
27	11	6·7-9·0 (8·1)	16·2-23·0 (20·3)
28	4	9·4-11·2 (10·3)	23·8-25·6 (24·5)
29	3	10·3-11·2 (10·8)	24·1-28·7 (26·3)
31	6	9·9-11·7 (10·9)	25·8-30·1 (28·3)
32	2	11·0, 11·8	28·7, 29·4
34	1	11·4	29·5
35	3	12·0-12·5 (12·2)	32·9-33·9 (33·2)
36	3	11·3-12·0 (11·7)	30·4-31·6 (30·9)
38	1	12·8	33·4
40	1	13·0	34·1

Hatching commenced after four days at Stage 20, but the peak was reached on the fifth day, and a few larvae hatched on the sixth day at Stages 20 to 21. By Stage 20 there were two pairs of external gills (each with only one or two branches), indistinct optic bulges, and prominent olfactory pits; the stomodeal depression had deepened and the ventral suckers had increased in size.

Maximum gill development occurred at Stage 22 with the anterior pair possessing one or two branches, and the posterior pair two or three. The optic bulges were still not distinctly demarcated and the corneas remained opaque. Stage 23 (material collected in the field on 1st October, 1972) exhibited greatly reduced external gills, clear corneas, well-differentiated olfactory pits (nares), lateral-line sense organs extending along the body to the caudal region, well-developed labia, and an open or partly open anal tube.

Oral ridges on which the labial teeth had developed were characteristic of Stage 25. The horny beak became pigmented and the extreme reduction of the ventral suckers diminished at this stage. Subsequent development mainly involved increase in size and proportions as recorded in Table 1.

In our description of the new species of the *L. citropa* complex we provide a detailed composite description of tadpoles at Stages 29 and 36. Here we report only those features apparent at Stage 35 of *L. citropa* that differ from those of the new species. Thus the anal opening is diagonal from the edge of the ventral fin, and tail depth is greatest just anterior to its mid-region.

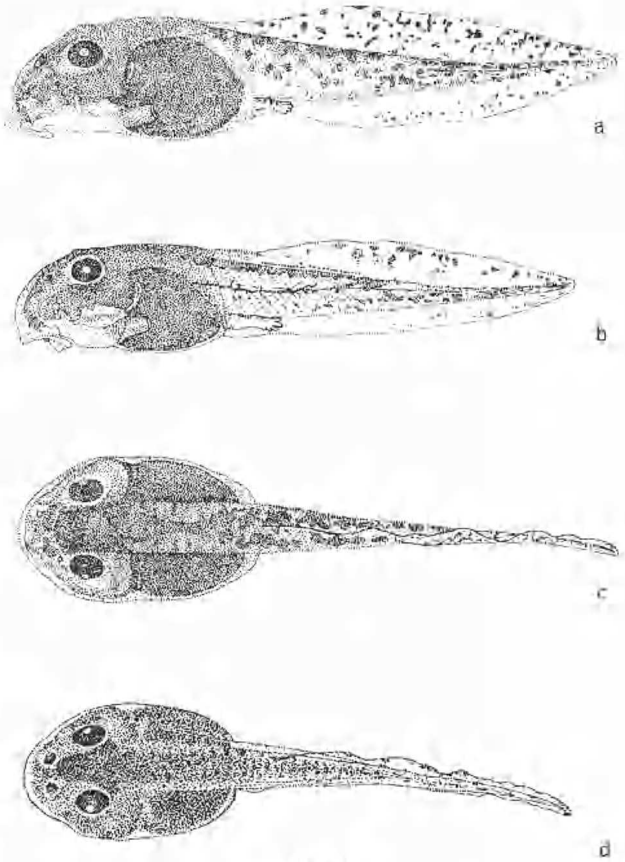

FIG. 3

(a and c) Lateral and dorsal views of larva of *Litoria citropa* at stage 35; (b and d) lateral and dorsal views of *L. glandulosa* at Stage 36.

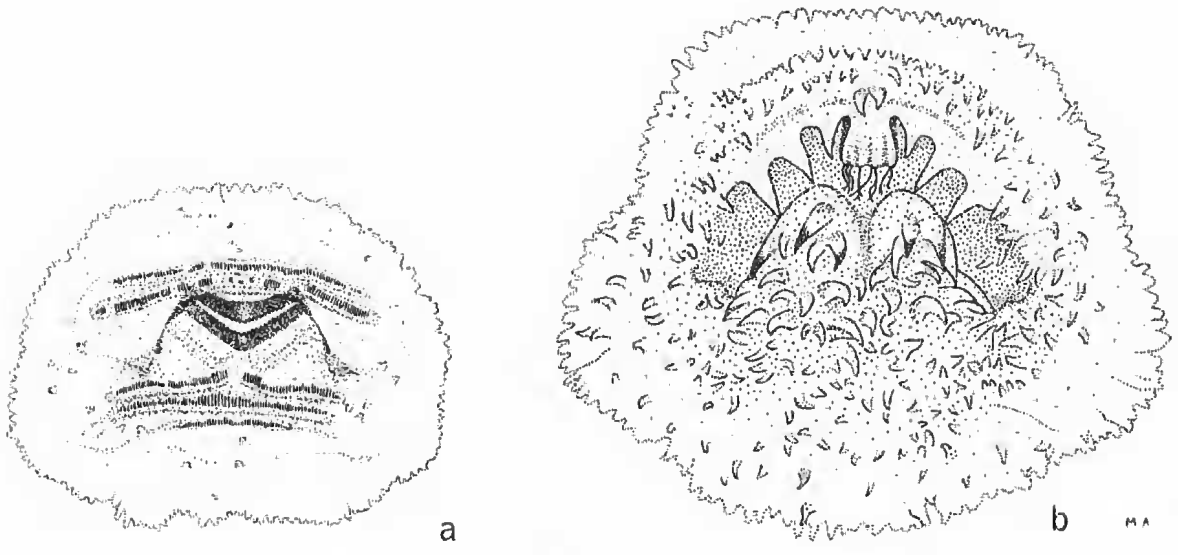

FIG. 4
Mouthparts of (a) *Litoria citropa*; (b) *L. glandulosa*

The mouth is ventral in position (Fig. 3a), and the labia are bordered by a single row of small papillae (Fig. 4a); only a few small papillae occur inside the labial border. There are two rows of upper labial teeth and three rows of lower labial teeth, of which the second upper is the longest, and the third lower the shortest. There is a medial gap in the second upper row and in the first lower row. Odd teeth were missing in the majority of the specimens examined. The beaks are pigmented, relatively shallow, and of almost equal depth with moderately-sized serrations.

In preserved specimens the dorsal surface of the body and the upper labium are dark brown with small areas of darker pigment. The orbital and narial regions are paler. The caudal musculature is cream and densely blotched with brown dorsally. The fins are transparent, but marked with scattered clusters of melanophores. The lateral line organs are unpigmented. In life the dorsal and lateral body surfaces have a uniform golden sheen, noticeably incomplete in its distribution at earlier stages (e.g., Stages 25-26).

Metamorphosis of tadpoles reared from the spawn laid on 6th November, 1972, was completed in January, February and March, 1973, indicating a larval life of from two to four months. Snout to vent lengths of eight newly metamorphosed specimens ranged from 11·9 mm to 14·3 mm (mean 13·1 mm).

Distribution: *Litoria citropa* extends from Aberfeldy in south-eastern Victoria to the Barrington Tops in New South Wales (Fig. 5).

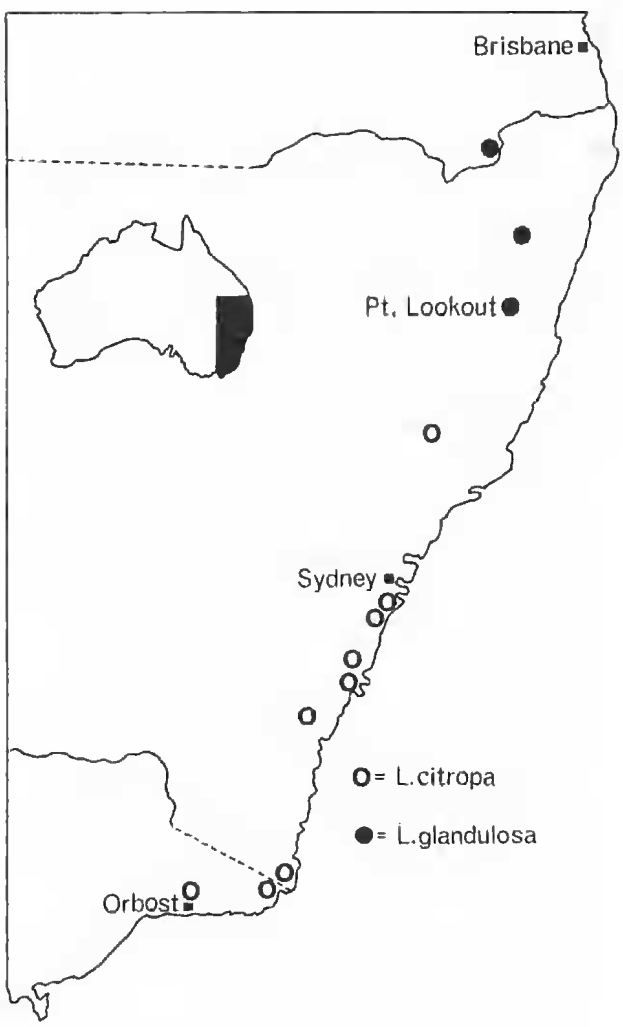

FIG. 5
Geographic distribution of the *Litoria citropa* complex. The close proximity of several adjacent localities is such that each individual locality cannot be shown on a figure of this scale.

Litoria glandulosa n. sp.

Holotype: S.A.M. R13504. A gravid female collected at Barwick Creek, Point Lookout, near Ebor, New South Wales, by M. Anstis on 24th January, 1973.

Definition: A moderately-sized species (adult females 45·8-50·4 mm S-V; adult males 34·5-40·3 mm S-V). Adults are characterised by an indistinct tympanum, and by the presence of a submandibular gland. The tadpole is unique amongst previously described Australian species in lacking tooth rows, and in possessing elongate tubercles and filaments within the buccal cavity (Fig. 4b).

Description of Holotype: The head is deep, bulbous and broader than long (HL/HW 0·91), its length is equivant to approximately one third of the total length (HL/S-V 0·34). The snout is not prominent; bluntly rounded when viewed from above and evenly rounded (but not projecting) in profile. The nostrils are orientated dorsolaterally; their distance from the end of the snout is slightly more than one-half the diameter of the eye. The distance between the eye and the naris is greater than the internarial span (E-N/IN 1·16). The canthus rostralis is clearly demarcated and straight, and the loreal region sloping but not concave. The eye is rather small and not prominent; its diameter equals the E-N distance. The tympanum is small and very poorly defined, there being no distinct tympanic annulus; the tympanum is separated from the eye by a distance about one-third of the eye diameter. The vomerine teeth are on two confluent elevations whose anterior borders are level with the posterior margins of the choanae. The tongue is broadly oval with a very weakly indented posterior border.

The fingers are long and slender with slight lateral fringes and prominent subarticular tubercles (Fig. 6a). There is only a trace of basal webbing between the fingers. The terminal discs are rounded and prominent.

The hind limbs are short and muscular (TL/S-V 0·52). Toes in decreasing order of length 4>5>3>2>1. Webbing between the toes reaches mid-way up the penultimate phalanx of the fifth digit, to a position slightly below the penultimate phalanx of the fourth digit. The terminal discs are prominent. There is a small oval inner and a very slightly developed rounded outer metatarsal tubercle (see Fig. 6b).

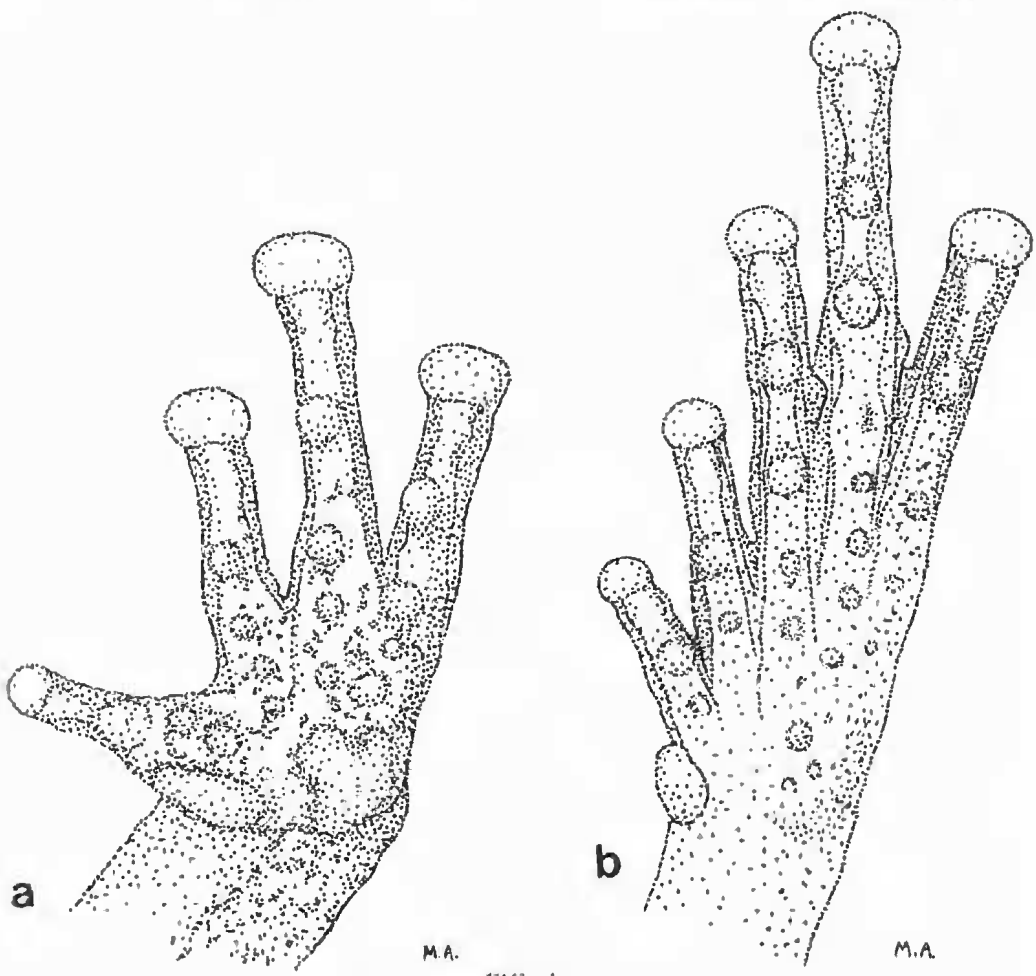

FIG. 6
(a) hand, and (b) foot of *Litoria glandulosa*.

The skin of the dorsal surface of the head and body is rather coarsely granulate. There is a very prominent supratympanic fold which obscures the upper portion of the tympanic region extending from the posterior corner of the eye to a position above the insertion of the forelimb. There is a slender supralabial gland and a narrow tarsal ridge.

There is a broad and prominent submandibular gland covered by smooth skin; the remainder of the ventral surface of the throat, pectoral region, abdomen and limbs is coarsely granulate.

The dorsal surface of the head, body and limbs is dark blue in life. The supratympanic fold is darker, and superior to it is an extremely irregular pale brown line merging into isolated creamish patches on the flanks. The supralabial gland is white and is preceded by a similarly coloured line extending to beneath the eye. A disrupted white line extends along the anterior portion of the labial margin.

The ventral surfaces are dull creamish in colour and densely stippled with black, particularly on the submandibular gland and breast. The posterior surfaces of the thighs are predominantly dull brown, sparsely spotted with cream. These cream spots are densest in the subcloacal area.

Dimensions: Snout to vent length 45·8 mm; tibia length 23·7 mm; head length 15·5 mm; head width 17·1 mm; eye to naris distance 4·3 mm; internarial span 3·7 mm; eye diameter 4·6 mm; tympanum diameter approximately 2·3 mm; diameter of terminal disc of third finger 2·3 mm.

Variation: There are 38 paratypes: S.A.M. R13505-10, collected at Barwick and Bullock Creeks, Ebor on 24th January, 1973; S.A.M. R13060 (11 juveniles); S.A.M. R13303, collected at Barwick Creek in January, 1973; S.A.M. R13626-39, A.M. R39498, collected at Point Lookout in May, 1973, all above specimens taken by M.A.; M.U.Z.D. 1991/68, 1992/68, 1997/68, 1999/68, collected at Point Lookout by M. J. Littlejohn, J. J. Loftus-Hills and G. F. Watson; M.U.Z.D. 1885/68 collected at 65 km E. of Glen Innes by Littlejohn, Loftus-Hills and Watson.

The adult male paratypes have snout to vent lengths ranging from 34·5 mm to 40·3 mm. All lack vocal sacs. The short limbs, relatively high E-N/IN ratio and broad head of the holotype are consistently demonstrated by the following ranges and means of proportions of these specimens: TL/S-V = 0·48-0·53, mean 0·50; E-N/IN 1·00-1·23, mean 1·14; HL/HW 0·87-1·00, mean 0·91.

Coloration varies only in the intensity of the blue dorsum and in the extent of the irregular lateral stripes and light markings on them. The posterior surfaces of the thighs are consistently darkly patterned. Snout to vent lengths of recently metamorphosed specimens ranged from 11·5 to 14·5 mm (mean 13·0 mm).

Coloration in life: Observations on an adult (S.A.M. R13678) indicated differences associated with activity. When active the dorsal surface of the head, body and limbs was brilliant green. The lateral stripe was dark brown on the side of the head, becoming paler in the supratympanic region and merging with a series of golden patches in the inguinal region. This lateral stripe was bounded superiorly by a gold line broadening on the body. The superior labial margin bore a cream stripe extending posteriorly to above the insertion of the forearm. The section of the head anterior and posterior to the eye and between these labial and lateral stripes was pale green. The iris was uniformly golden. There were rows of gold and brown flecks on the borders of the limbs. The hands and feet were mottled with gold and green. The ventral surfaces were a creamish white; the submandibular gland had a faint yellow hue. The axilla, and inguinal areas and the anterior and posterior surfaces of the hind limbs were a translucent deep yellow.

When the frog was at rest the dorsum was usually very dark brownish-green, the lateral stripe and associated patches a rusty brown and the labial stripe grey. The iris was golden above the pupil, brown below it. The ventral surfaces were generally dusky brown.

In other specimens dorsal coloration ranged from olive with uniform dark green mottling (or mottling confined to the limbs), green with large, discrete gold patches (J. de Bavay, pers. comm.) to gold or brown so that the lateral stripe was scarcely discernible. Those found in green vegetation were inevitably bright green, whether collected by day or night. The colour of individuals found beneath rocks or logs varied from dark brown to almost any shade of green. In captivity most frogs were dark whilst at rest during the day and bright green whilst active at night.

Habitat: The specimens collected or observed by M.A. were taken adjacent to creeks and rivers in cool, montane forest within 10 km of Point Lookout, and at altitudes of 1 350-1 450 metres. These water courses are:—

(*a*) Barwick River, consisting of moderately deep pools (containing submerged plants), separated by shallow flowing sections and waterfalls. The floor of the river is predominantly basalt.

(*b*) Little Styx River, which is similar to Barwick River, but appreciably broader.

(*c*) Bullock Creek, which differs from Barwick River only in its generally smaller dimensions and predominantly granite base.

(*d*) Spring Creek, the smallest of all four watercourses, with a sandy floor over a basalt base.

Amongst the vegetation on the banks were species of *Juncus*, *Epacris*, *Leptospermum*, *Ranunculus*, *Pterostylis* and various ferns. Areas of sphagnum were present. The dominant species of tree was *Eucalyptus pauciflora*, which was replaced by *Nothafagus moorei* at higher altitudes.

Adult behaviour: During the periods of observation the species was found amongst vegetation adjacent to the watercourses, beneath rotten logs, under bark on trees or amongst rocks and low vegetation (particularly *Juncus*).

In May, 1973, 14 adult males, one female and one juvenile were found together under a rotting log approximately three metres long and one metre across. We conclude from their sluggish behaviour that they had aggregated to hibernate communally. To our knowledge this represents the first report of a possible communal hibernaculum for frogs in Australia.

Data on breeding behaviour are lacking. However, we have evidence to indicate an exceptionally long breeding season. For example, the sighting of amplexal pairs on the Barwick River in mid-December, 1971 (J. Barker, pers. comm.), indicates larval development during the summer months when water temperatures reach their annual maxima. The dates of collection of the stages of larvae reported below are consistent with ova being deposited in November-December.

In apparent conflict is the finding of a gravid adult female in May in the hibernaculum. The entire body cavity was filled with large pigmented eggs up to 2·1 mm in diameter and, perhaps more significantly, the oviducts were greatly enlarged and extensively convoluted. The specimen was found in breeding condition at a time when ground temperatures were so cold as to make it lethargic. We therefore believe that at least this female would have been in breeding condition at the conclusion of hibernation in the following spring.

Newly metamorphosed specimens of *L. glandulosa* were collected in December, supporting our belief that some individuals do breed in the spring.

The mating call has not been recorded on tape. It consists of a series of several, moderately low-pitched notes initially increasing in volume and rate, and finally slowing. M.A. likens it to: "orak-orak-orak . . . .".

Life History: The spawn and early stages of development are unknown. Tadpoles in Stages 25 to 43 were observed in the Barwick River on 20th December, 1972, in a shallow, slowly moving section just beneath a deep pool. Most larvae appeared to be feeding over the red silt covering stones on the stream bed. When disturbed they swam under rocks. Stages 29 to 36 were collected on 25th January, 1973, from a physically similar section of Spring Creek but in an area where the floor was covered with pale sand, against which tadpoles were well camouflaged. Some were amongst the roots of water plants, but others lay in exposed areas, occasionally moving to the shallower sections of the pool.

Measurements and ratios of proportions on the above series are summarised in Table 2. The following description of larval morphology is a composite one based on specimens at Stages 25-43.

TABLE 2

MEASUREMENTS OF LARVAE OF L. GLANDULOSA AT VARIOUS STAGES AT BARWICK RIVER COMPARED WITH SPRING CREEK WHICH ARE SHOWN IN PARENTHESIS

Stage	Body Length (mm)	Total Length (mm)	Sample Size
25	4·8	14·3	1
26	5·3	13·5	1
29	10·2 (8·5)	26·2 (20·6)	1 (1)
30	9·9, 10·1	23·6, 23·8	2
31	10·4	24·8	1
33	9·4 (9·6)	23·2 (25·0)	1 (1)
34	(10·2-11·0)	(25·3-29·0)	(3)
35	11·0 (9·9-10·9)	26·2 (26·1-30·0)	1 (7)
36	10·9-11·2 (11·0, 11·6)	26·2-17·4 (30·2, 30·5)	3 (2)
37	11·4	29·0	1
38	10·7, 11·7	29·1, 31·0	2
39	11·0-11·7 (11·2)	29·7-32·4 (30·5)	4 (1)
40	11·0	29·5	1

The snout is evenly rounded in lateral and dorsal profiles (Fig. 3b, d). The nares are closer to the tip of the snout than to the eyes, dorsal in position and directed anterolaterally. The eyes are in a dorsolateral position. The body is broadest at a position corresponding to the level of the eyes and is broader than deep. The spiracle is sinistral, ventrolateral in position and is slightly further from the tip of the snout than from the anus. The anus is dextral, opening adjacent to the edge of the ventral fin.

The tail is a moderately thick structure deepest at about the anterior one-third, narrowing posteriorly and is terminally rounded. The lateral lines are pigmented and the lateral line organs are numerous and narrowly spaced.

The oral disc is ventral in position and is in the form of a funnel marginally surrounded by a row of small papillae (Fig. 4b). The area within this funnel is occupied by numerous finely-pointed papillae projecting ventrally and occupying the greater part of the lumen. From the most superficial to the deepest, the lengths of the papillae increase so that all terminate in the form of spikes near the level of the disc margin.

On the inner edge of the lower labium, adjacent to the mid-line, is a variable number (2-6) of large, black papillae. There are no tooth rows and the horny beak is small, unpigmented and located far posteriorly. There is a flat white structure projecting from the centre of the upper beak forward and then inclined ventrally, and terminally divided into from four to seven tooth-like structures, each of which bears from one to four fine, hair-like black filaments. Some of the filaments are branched. In many specimens all filaments have broken off leaving a white basal core. On each side of this projecting structure is a row of three large, pointed papillae.

In life the dorsal surface of the tadpole is brown with an irridescent golden sheen. Small, scattered, dark brown spots are most conspicuous in later stage tadpoles. The areas around the eyes and nares are least pigmented. The fins are transparent, but for dark brown flecks, densest on the superior margin. The caudal musculature appears cream in transparency. In preservative the golden irridescence of the body is lost and the specimens appear darker.

At metamorphic climax body lengths range from 12·0 mm to 12·8 mm. In life frogs at this stage are brown with a gold sheen. The lateral stripe, so conspicuous in adults, extends posteriorly only to the insertion of the arm. The dorsum bears numerous flattened tubercles which become progressively less conspicuous in older specimens.

Distribution: *Litoria glandulosa* probably replaces *L. citropa* on the Great Dividing Range of northern New South Wales (Fig. 5). G. Ingram (pers. comm.) reports collecting specimens in eastern Queensland just north of the New South Wales border which were probably *L. glandulosa*. Three specimens were taken adjacent to the Girraween National Park, south of Stanthorpe. The description of the habitat (a small creek descending from extensive rock formation) is similar to those at which *L. glandulosa* has been collected by M.A.

COMPARISON WITH OTHER SPECIES

Distinguishing characters for adult *L. glandulosa* and *L. citropa* are compared in Table 3.

TABLE 3

SUMMARY OF MAJOR DISTINGUISHING FEATURES OF L. GLANDULOSA AND L. CITROPA

Character	L. glandulosa	L. citropa
S-V (males) mm	34·5-40·3	46·9-56·6
S-V (females) mm	45·8-50·4	56·5-56·9
Tympanum	hidden	distinct
Vocal sac	absent	present
Bones	unpigmented	unpigmented or violet
Larval labial teeth	absent	present
Larval oral disc papillae	elongate	short
Larval horny beak	small, white	large, black

Adults of *Litoria glandulosa* can be easily distinguished from all other species of *Litoria* except *L. citropa* by its possession of a very large submandibular dermal gland and prominent supratympanic fold. Only *L. caerulea* has comparable (and in fact more extensive) supratympanic fold, but it is a much larger and far more robust animal and lacks the dark lateral band and gold lateral line of *L. glandulosa*, and has broadly webbed fingers.

DISCUSSION

Absence of labial teeth in hylid tadpoles has previously been reported only for the Neotropical Region (Martin and Watson, 1971), where, in the genera *Amphignathodon*, *Cryptobatrachus*, *Gastrotheca* and *Hemiphractus* larvae are carried on the backs of parent females for at least part of their development. Species of *Hyla* lacking labial teeth usually have enlarged horny beaks. The absence of both labial teeth and of a pigmented horny beak in *L. glandulosa* appears unique.

Until now the newly described species *L. glandulosa* has been included within *L. citropa* and, although morphological comparison of the adults of the populations indicates two distinct species, it appears that they are closely related to one another. Our finding that the larval mouthparts of *L. citropa* (*sensu stricto*) are of a pattern common to many Australian *Litoria*, whereas those of *L. glandulosa* are so different therefore poses problems of interpretation.

There are far from adequate data for assessing the ancestry and phylogenetic relationships of Australian hylids. In view of the extent of morphological divergence currently encompassed within *Litoria*, it can be predicted with some confidence that *Litoria* will be ultimately shown to constitute several distinct genera.

If *L. citropa* had not been known and we were here describing *L. glandulosa*, there would be adequate data from our knowledge of adult and larval morphology to place it in a new genus. The purpose of such a step being to demonstrate that *L. glandulosa* is so different from all species recognised previously, the erection of a separate genus would be a useful and logical step demonstrating the extent of divergence from *Litoria* as currently constituted.

In the absence of any information on larvae, subsequent discovery of *citropa* adults would not have posed a problem. The general morphology and particularly the possession of the submandibular dermal gland would have justified its association with *glandulosa* in the new genus. Subsequent discovery and identification of the tadpole of *citropa* with its generalised mouth-parts would raise the sort of questions that we now actually face.

There seems no reason to doubt that the direction of larval evolutionary change is from the generalised hylid pattern of *citropa* to the bizarre lotic adaptation of *glandulosa*. Nevertheless, the extent of the adaptation involves major morphological changes: loss of all labial teeth rows, and pigmentation of the horny beak, and the development of oral disc tubercles with keratinised tips. Whether or not the central black filaments suspended anterior to the pharynx involve particle filtration, or have a sensory function, is immaterial to the assumption that their evolution constituted an extremely major evolutionary shift.

We do not dispute Watson and Martin's (1971) contention that hylid larval features are of value in assisting studies of phylogenetic relationships. However, our observations demonstrate that divergence in adult and larval morphology is not necessarily complementary.

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